

FLOWER ABUNDANCE IN A POPULATION OF SKY  
LUPINE (*LUPINUS NANUS*) OVER THREE YEARS IN  
CENTRAL COASTAL CALIFORNIA

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ABSTRACT

Three consecutive years of monitoring *Lupinus nanus* bloom in central California demonstrates over an 11 fold difference in peak inflorescence numbers among years. Bloom duration was longest during those years that had the highest peak blooms. The level of peak annual bloom did not necessarily correlate with the total annual rainfall amount, but instead with the amount of rainfall during the period of January through March when seed induction and germination occur. High annual variation in the numbers of available flowers (during times when few other flower species are available) may have profound implications for early season bee fauna that utilize pollen of this species to complete their life cycle. These pollinator fluctuations might affect the pollination success of *L. nanus* and may ultimately produce the facultatively autogamous mating system observed in this species. In addition, the observed variation in flower abundance of this nitrogen-fixing species may have implications for nutrient availability within the ecosystem, thereby influencing the abundance and productivity of other plant species.

*Lupinus nanus* Benth. is an abundant annual herb, up to 50 cm tall, which forms dense patches in open or disturbed areas within old-fields, grasslands and oak savannas in California (Dunn 1956; Hickman 1993). A number of studies have documented large genetic variability within *L. nanus* for reproductive traits, such as flowering time, flower size, flower color and pollen production (Harding and Horovitz 1967; Horovitz and Harding 1972; Harding et al. 1974). The plant is also facultatively autogamous (Karoly 1992) and there are genetic differences between populations in outcrossing rates (Horovitz and Thorp 1970; Horovitz and Harding 1972). There are also differences between populations in their required rates of pollinator visitation and, in some cases, pollinator availability can limit reproductive success (Karoly 1992).

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Plant population sizes can vary substantially from year to year and in California this variability is often related to both the amount and the timing of rainfall (Harding 1970; Pitt and Heady 1978; Allison 1992). Indeed, Dunn (1956) reported that populations of *Lupinus nanus* "vary in size from year to year and may even disappear at intervals depending upon the weather during the period of germination." Here we report three consecutive years of flower abundance levels for *L. nanus* and discuss the implications of bloom variability for insect and other plant populations that depend upon pollen and nitrogen produced by lupine populations.

#### METHODS

*Study site.* Our study population of *Lupinus nanus* was located at the Hastings Natural History Reservation in Monterey Co., 42 km SE of Carmel in coastal-central California (36°23'N, 121°33'W). The climate of this region is characteristic of a Mediterranean area, with hot, dry summers and moderate wet winters (Major 1977). The mean annual precipitation is 538 mm, but precipitation varies from 261 mm to 1112 mm. More than 90% of the rain falls between November and April (Fig. 1). Records of rainfall during the three year lupine monitoring period were recorded at the Hastings weather station, located about 500 m northeast of the study population. Daily values were used to calculate monthly mean maximum, average and minimum values of temperature and total monthly rainfall during our study period.

*Lupine phenology.* Bloom abundance in our study population was monitored with three parallel transects approximately 30 m apart. Sampling plots were set at 5 m intervals along each transect and were one m<sup>2</sup> in area. All of these transects were bisected by a creek (Big Creek) so that eight sampling plots extended perpendicularly from either side of the creek, producing a total of 48 plots. As an estimate of total bloom, plots were censused on a weekly basis for numbers of inflorescences with at least one open flower. The same plots were used each year of the study and were reused by relocating metal spikes set in the ground at each sampling plot. Sampling days were Mondays in 1990 and Sundays in 1991 and 1992. Transects were monitored as long as flowering occurred in the sampling plots.

*Bee diversity and phenology.* Collections of bees were made at various times during the bloom period of *L. nanus* from 1989–1992 with a hand-held insect net. In addition, we tested for seasonal synchrony between *L. nanus* and one of its common bee visitors, the cavity nesting solitary bee *Osmia lignaria* (Megachilidae) by arraying sampling units in the vicinity of our lupine study plots during 1990; this bee ordinarily nests in small cavities found naturally in

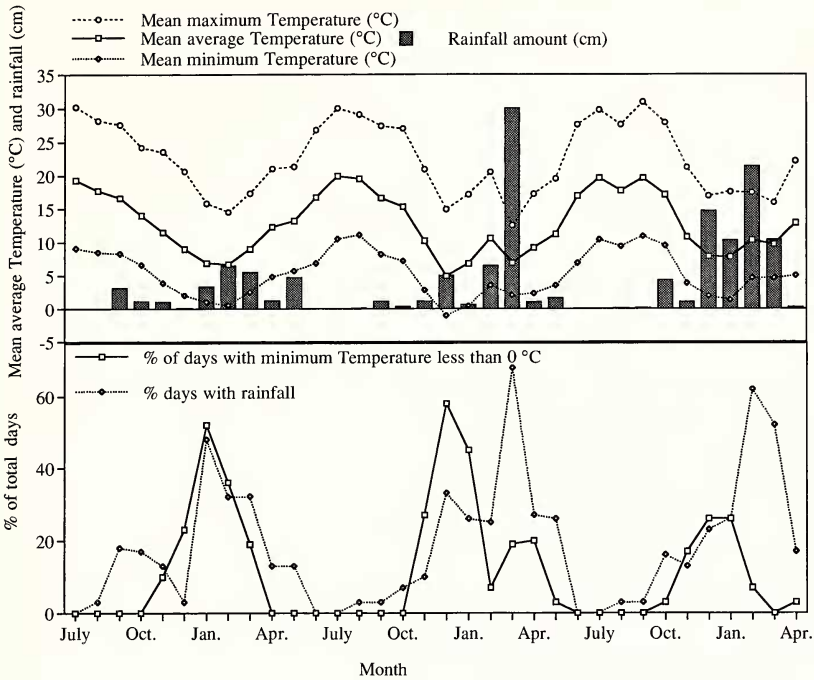


FIG. 1. Graphs of (a) precipitation as well as mean maximum, mean average, mean minimum temperatures and (b) the % of days per month with rainfall and the percentage of days per month with a minimum temperature less than 0°C at Hastings.

and around oak forests, and will readily nest in artificial sampling units made from wooden subunits called "trap-nests" (Krombein 1967). Each trap-nest had dimensions of 12.0 × 2.5 × 2.0 cm, with a single hole drilled to a 10 cm depth down its length. Four trap-nests for each of three hole diameters (0.50, 0.65 and 0.80 cm) were systematically arranged within a 5.0 × 12.0 × 12.0 cm sampling unit and hung with wire from nails at 1.5 m heights on living oak trees near Big Creek. Fifteen sampling units were spread approximately equidistantly along each of three belt transects within the creek basin ( $n = 45$ ). Field replacements were made on the same day of each week (Sundays), one day before lupine censusing.

#### RESULTS AND DISCUSSION

We found striking, statistically significant, differences in flower abundance among years, with the peak in the average number of open inflorescences per m<sup>2</sup> ranging from 5.5 in 1990 to 61.0 in 1991 (One-way Anova,  $F$  ratio = 19.4, 2 degrees of freedom,  $P < 0.000$ ). An average of 46.2 inflorescences per m<sup>2</sup> was recorded as the peak

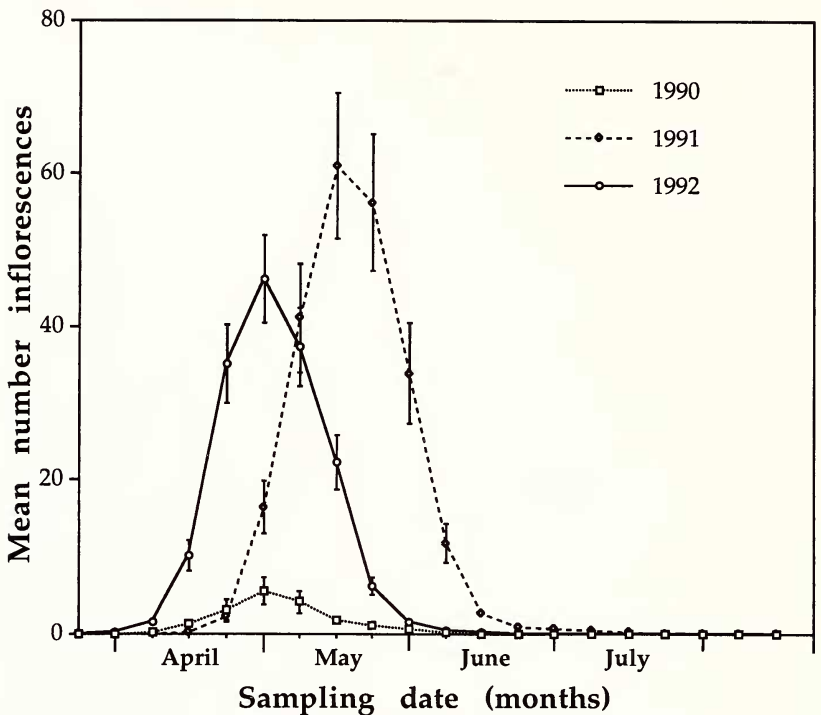


FIG. 2. Mean number of inflorescences per plot of *Lupinus nanus* in three years. Given are the means  $\pm$  1 SE. Sampling was at weekly intervals beginning on March 26 of 1990, March 24 of 1991 and March 22 of 1992.

in 1992 (Fig. 2). The total rainfall during 1990 was 26.5 cm, 47.1 cm during 1991 and 61.5 cm during 1992. The fact that the year with the highest peak number of flowers (1991) did not occur during the year of greatest total rainfall (1992) suggests that not only annual rainfall, but also the timing of heavy rainfall periods within years influences germination levels and subsequent flower abundances.

Seeds of *Lupinus nanus* do not necessarily germinate each year and do not have an inner dormancy (Harding 1970). Minimum temperature is therefore not likely to influence germination. Rather, they depend on a hard seed coat which requires decomposition or abrasion for the control of germination (Dunn 1956). In general, decomposition in Mediterranean ecosystems is strongly influenced by the availability of water (Hart et al. 1992), thus the amount of water during the time of germination is likely to not only directly influence seed germination, but also to influence microbial populations that decompose organic matter. The number of days from seed imbibition to flowering in *L. nanus* has been reported to range from 46 to 70

TABLE 1. COMPARISON OF ONSET, PEAK AND END BLOOM DATES FOR *LUPINUS NANUS* 1990–1992.

Year	Onset date	Peak date	End date	Duration
1990	9 April	30 April	11 June	9 weeks
1991	14 April	12 May	28 July	14 weeks
1992	29 March	26 April	21 June	11 weeks

days (depending on genotype), with an average of 54 and a median of 52 days in a greenhouse study (Horovitz and Harding 1972), which is consistent with field data collected by Dunn (1956). This implies that seed induction and germination occur during the period of January to March in our study population. We see no striking difference in rainfall during this period between the 1990 and 1991 flower seasons and the difference between peak flower abundance levels of these two years was the least of all three years, supporting the view that this early period of the year is important for germination. In addition, the period of December to January of 1992 was much wetter than in the previous two years and the onset and peak flowering dates were also earlier that year (Fig. 1, Table 1). Flower abundance during 1991 was probably most influenced by continuous rain storms during the month of March (Fig. 1). These probably wetted the top soil levels (where the seeds are present) for a longer period and may have resulted in a build-up of microbial populations in the soil (increasing seed coat decomposition) as well as increased moisture levels for germinating seeds. An alternative explanation of the observed differences in flower abundance is that the germination rates remained constant and that the seedling to adult survival rate varied strongly between the years. However, *L. nanus* does have a substantial seedbank (Harding 1970) and depends on a hard seed coat, and not an inner dormancy for the control of germinating (Dunn 1956). In addition, drought is likely to be the main factor influencing the survivorship of the seedlings and we found no striking drought period in 1990, which could have caused a large mortality in that year. These factors support the hypothesis that differences in germination are the cause of the observed differences in flower abundance between the years.

*Lupinus nanus* is reported to be autogamous to a large extent (Dunn 1956; Karoly 1992). However, the mating system of this species is strongly influenced by the availability of pollinators as documented in outcrossing studies (Horovitz and Harding 1972; Karoly 1992). We have thus far recorded 20 different bee species visiting *L. nanus* at Hastings (Table 2). One of these, *O. lignaria*, is a common cavity nesting solitary bee species that forages from early April until late May (Barthell 1992; Thorp et al. 1992). Females of this species are known to shift sex ratios of their progeny from female-

TABLE 2. BEE SPECIES OBSERVED VISITING *LUPINUS NANUS*.

Family	Species
Halictidae	<i>Halictus farinosus</i> Smith
Andrenidae	<i>Andrena atypica</i> (Cockerell) <i>Andrena</i> sp.
Megachilidae	<i>Osmia lignaria propinqua</i> Cresson <i>Osmia regulina</i> Cockerell <i>Osmia tristella</i> Cockerell <i>Osmia atrocyanea</i> Cockerell <i>Osmia nemoris</i> Sandhouse <i>Osmia zephyros</i> Sandhouse <i>Osmia</i> sp. <i>Panurginus</i> sp.
Anthophoridae	<i>Habropoda depressa</i> Fowler <i>Habropoda</i> sp. <i>Synhalonia</i> sp. 1 <i>Synhalonia</i> sp. 2
Apidae	<i>Apis mellifera</i> Linnaeus <i>Bombus caliginosus</i> Cresson <i>Bombus edwardsii</i> (Frison) <i>Bombus vosnesenskii</i> Radoszkowski

to male-biased proportions as floral resource quality decreases over the nesting season, suggesting that pollen availability is an important determinant in the bee's life history strategy (Torchio and Tepedino 1980).

*Osmia lignaria* females appear to rely upon *L. nanus* for pollen (Barthell et al. 1996). In addition to the distinctive orange pollen found on foragers at flowers and in their nest cells (dissected from trap-nests), a striking coincidence in nest cell and flower abundance peaks were observed in 1990 (Fig. 3). A similar coincidence was noted the following year (1991) in an unrelated study conducted in the same area (Barthell 1992), suggesting that *O. lignaria* may track the bloom phenology of *L. nanus* during its nesting season at Hastings. The large depressions in annual, peak flower abundances that we observed in our study could therefore influence the reproductive success of potentially resource-sensitive pollinators such as *O. lignaria* and thereby lower the availability of pollinators in subsequent years. The facultative autogamous habit of this species may circumvent such potential pollinator limitation, while maintaining sufficient variability through outcrossing to prevent inbreeding.

Lupine species are often abundant in early successional stages of grasslands in California (Heady 1977) and can locally contribute a substantial amount of nitrogen to the ecosystem by fixing atmospheric nitrogen (Woodmansee and Duncan 1980; Fahey et al. 1985; Halvorson et al. 1992). Nitrogen is considered to be the most limiting nutrient in these grasslands (Woodmansee and Duncan 1980;

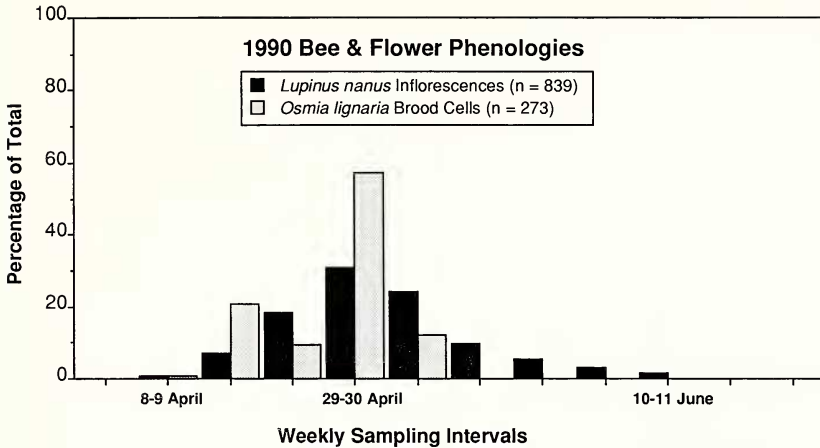


FIG. 3. Weekly proportions of the total number of *Lupinus nanus* inflorescences and nest cells of *Osmia lignaria* during 1990.

Menke 1989). Therefore, variation in lupine abundance not only influences the insect populations depending on them for pollen, but may also influence the availability of nitrogen, thereby influencing ecosystem productivity and composition.

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